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Larval Biology and Ecology of *Photuris* Fireflies (Lampyridae: Coleoptera) in Northcentral Florida[1]

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ABSTRACT: Larvae of *Photuris* fireflies having a reddish-brown or rufous ground color (red larvae) were collected in hardwood leaf litter in drier woodland situations. They were commonly collected in August and September but were seldom found at other times. Only 2 red larvae pupated and produced adults which were identified as *Photuris congener* LeConte. Most *Photuris* larvae (non-red larvae) had a gray or tan ground color and were collected throughout the year. Non-red larvae produced adults of several morphologically cryptic undescribed firefly species which are currently known by code names. *Photuris* "A" and "V" fireflies were reared from larvae collected throughout the year from wet areas. *Photuris* "B and D" fireflies were reared from larvae collected primarily in spring and fall from a wet wooded area. *Photuris* "W" fireflies were reared from larvae collected in rotten logs.

Cold treatments and light-dark cycle changes failed to induce red larvae to pupate. Cold treatments and short-day light cycles delayed pupation of non-red larvae. Non-red larvae collected in October, November, and December required 60–140 days to reach pupation while larvae collected at other times pupated within 25–70 days.

Photuris larvae rested, molted and pupated in several types of earthen chambers and excavations. These larvae were predator-scavengers which fed on a variety of small soft-bodied organisms and fruits. Of 17 prey records for red larvae, 5 were snails or slugs, 11 were insects, and 1 was a ripe berry. Of the 4 prey records for non-red larvae, 1 was an earthworm, and 3 were berries.

Fireflies of the genus *Photuris* are common throughout much of the New World and occur in a variety of habitats (Barber, 1951). The flash behavior of these fireflies indicates that there are numerous morphologically cryptic species in North America (Barber, 1951; Lloyd, 1969), however, the flash behavior of these fireflies is more complex than that of other American fireflies so the taxonomy of this genus has not been resolved (Lloyd, 1969). Our understanding of the biology of immature *Photuris* fireflies is also incomplete and most of the available information applies to several species occurring in northeast United States (Williams, 1917; Hess, 1920; Keiper and Solomon, 1972; McLean et al., 1972).

In northcentral Florida at least a dozen species of *Photuris* occur in a variety of habitats. Most of these species are currently undescribed and their identities are based on the flash behavior of free-flying adult males (Lloyd, 1969). Many of the species cannot be reliably identified by morphological characteristics at this time. Potential differences that might occur in the biology of the immature forms of these different species have not been investigated. Barber (1951) suggested that "feeding habits (of larvae) must differ between marsh-inhabiting species and other

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field or upland species." Additional data on the biology of the immatures of these fireflies would help define species and improve our understanding of fireflies of the genus *Photuris*. The biology and ecology of the immature stages of several fireflies of the genus are reported in this paper.

Methods and Materials

Larvae of *Photuris* were collected from numerous localities and habitats around Gainesville, Florida 1970–1976 in an effort to collect immatures of as many species as possible. Most of the larvae were collected in the Lake Alice-Medical Plant Garden area on the campus of the University of Florida. At Site "A" (Lake Alice) larvae were collected on the shore and on mats of floating vegetation near shore where the larvae appeared to be stranded after a rise in water level. At Site "M" (Medical Plant Garden) larvae were collected in 3 areas: the "wet area", the "dry area", and the "wooded area". The wet area was always damp and had standing water after a rain. The grass and weeds in this area were mowed several times each year. The dry area was slightly higher and better drained. The grass in this area was also mowed. This area was usually covered with leaves from deciduous trees. The wooded area was located between the garden and the lake and differed from the 2 previous areas in that the underbrush had not been cleared and the ground was covered with leaf litter. This area flooded when the water level in the lake was high. At Site "R" (Archery) and Site "G" (Gun Club) larvae were collected in the wet ditches along roads which passed through mesic hardwood forests. At Site "N" (Newnans Lake) larvae were collected in the ditch along a highway (roadside collections) and in the mature mesic hardwood forest along this road (woods collections). Collections from additional sites are combined for this discussion.

Glowing larvae were collected at night on warm evenings after a rain. The collection areas were visited throughout the year. Collected larvae were reared individually in 177 ml babyfood jars containing 10–15 mm of moist sifted sand. They were fed pieces of chicken liver (frozen) or cut-up insects at irregular intervals. Larvae were maintained individually until adults emerged or the larvae died. Molted skins and emerged adults were preserved.

Adult *Photuris* reared from field-collected larvae were identified using morphological characteristics furnished by J. E. Lloyd (Lloyd, 1969, and pers. comm.). Most of the species of *Photuris* occurring in northcentral Florida are undescribed and are currently known only by code names (Lloyd, 1969, and pers. comm.). The following species or species groups are used here: *Photuris congener* LeConte, a single morphologically distinct species; *Photuris* "A", a single morphologically distinct species; *Photuris* "B + D", a combination of 2 species currently known as *Photuris* "B" and *Photuris* "D", *Photuris* "W", a combination of 2 species currently known as *Photuris* "WD" and *Photuris* "WM", *Photuris* "V", a combination of at least 3 species currently known as *Photuris* "BR", *Photuris* "GR" and *Photuris* "J-3-4" (*versicolor* group).

There was considerable variation in pigmentation among the larvae collected at different seasons and at different locations. Most *Photuris* larvae had a gray or tan ground color, but one group of larvae had a pronounced reddish-brown or rufous ground color. These two groups of larvae seemed to have different ecological requirements and they will be discussed separately as "non-red" and "red" larvae.

Table 1. Seasonal occurrence of *Photuris* larvae in Alachua Co. Florida.

Collection site (habitat)	Month of collection[a]												
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Red larvae													
M (dry)	0	2	0	0	0	0	0	36	20	0	3	0	61
G (roadside)	—	—	0	—	—	—	—	—	—	1	—	—	1
N (woods	0	0	0	—	—	0	0	18	—	—	—	—	18
Total red larvae	0	2	0	0	0	0	0	54	20	1	3	0	80
Non-red larvae													
M (wet)	1	13	56	26	0	0	12	23	0	6	69	24	230
M (woods)	0	0	42	6	0	0	1	6	5	0	3	0	63
A (shore)	0	1	8	2	5	3	1	17	0	1	0	6	44
G (roadside)	—	—	—	—	1	—	—	—	—	10	—	—	11
R (roadside)	—	—	—	—	—	—	—	10	—	—	—	—	10
N (roadside)	30	—	—	—	—	—	—	25	—	—	—	—	55
N (woods)	14	1	14	—	—	—	—	0	—	—	—	—	29
Other sites (roadside)	—	—	2	—	—	4	1	—	—	—	—	—	7
Total non-red larvae	45	15	122	34	6	7	15	81	5	17	72	30	449
Number of collections													
Sites M and A	1	6	7	9	3	2	3	7	2	1	1	1	43
Other sites	3	2	4	—	1	1	—	3	1	3	—	—	18
Total collections	4	8	11	9	4	3	3	10	3	4	1	1	61

[a] Number of larvae collected or number of collections made, "0" indicates no larvae were found, "—" indicates no collections were made.

A total of 44 red larvae collected on 17, 18, 21 Aug., 11, 25 Sept., and 4 Nov. 1971, and 93 non-red larvae collected 4 Nov. and 6 Dec. 1971, were divided into 4 treatment groups on 16 Dec. and utilized in the following photoperiod experiment. Groups 1 and 2 were placed in a refrigerator and reared for 36 days at 2–14°C and 10:14 h light-dark cycle (short day). After the cold treatment the larvae were transferred to light boxes where they were maintained at 20–25°C; group 1 was exposed to 15:9 h light-dark cycle (long day) and group 2 was exposed to 10:14 h light-dark cycle (short day). Groups 3 and 4 were placed in the light boxes on 16 Dec. and maintained at 20–25°C: group 3 was exposed to 15:9 h light-dark cycle and group 4 was exposed to 10:14 h light-dark cycle.

Results and Discussion

Photuris larvae were frequently found after dark glowing periodically as they crawled in leaf litter. Collections were made on a total of 61 dates during each month of the year (Table 1). Larvae were common when leaf litter was wet, particularly after a rain that followed an extended dry spell.

ECOLOGY OF LARVAE: Red *Photuris* larvae were found in hardwood leaf litter in the drier situations at Sites "M" and "N". Large numbers of red larvae were collected in fall, August through November (Table 1). Only 2 larvae completed development and produced adults; they were identified as *Photuris congener* (Table 2).

Table 2. The species distribution of *Photuris* fireflies reared from larvae collected from different sites (habitats) and collected at different times of the year.

	Photuris congener	*Photuris* A	*Photuris* B + D	*Photuris* W	*Photuris* V	Totals
Collection site (habitat)						
M (wet)	0	82	24	0	10	116
M (dry)	1	0	0	0	0	1
M (woods)	0	8	28	0	0	36
A (shore)	0	20	2	0	0	22
G (roadside)	1	0	0	0	9	10
R (roadside)	0	0	3	0	1	4
N (roadside)	0	1	0	0	8	9
N (woods)	0	0	0	14	0	14
Other sites (roadside)	0	0	0	1	1	2
Total	2	111	57	15	29	214
Month of collection						
January	0	0	0	11	0	11
February	1	4	2	0	3	10
March	0	12	38	4	1	55
April	0	8	2	0	0	10
May	0	0	0	0	1	1
June	0	2	0	0	0	2
July	0	5	0	0	3	8
August	0	17	3	0	9	29
September	0	2	1	0	0	3
October	1	1	2	0	9	13
November	0	38	8	0	2	48
December	0	22	1	0	1	24
Total	2	111	57	15	29	214

Non-red larvae were collected throughout the year but they were most common in early spring and in fall and were scarce during the summer (Table 1). These larvae were found at many sites and usually in areas that remained wet most of the year.

The adult fireflies reared from non-red larvae belonged to a number of different species. *Photuris* A fireflies were reared from larvae collected throughout the year and most frequently from larvae collected in the wet areas at Sites "M" and "A" (Table 2). They seemed to be most common in areas where the soil was wet all year and flooded occasionally.

Photuris B + D fireflies were reared from larvae collected in early spring, February through April, and in the fall, August through December (Table 2). They were reared most frequently from larvae collected in the wooded area and the wet area at Site M. Most larvae collected in the woods in March produced *Photuris* B + D fireflies.

Photuris W fireflies were reared from larvae collected in January and March (Table 2). They were reared from larvae collected from 2 different rotting logs. Larvae of *Photuris* W were collected only in rotten logs and probably occur only in this habitat.

Table 3. Development of *Photuris* larvae exposed to several temperature and light/dark cycles.

	Treatment groups			
	Group 1	Group 2	Group 3	Group 4
Experimental treatments				
First period				
Temperature	cold	cold	room	room
Light/dark cycle	short day	short day	long day	short day
Second period				
Temperature	room	room	room	room
Light/dark cycle	long day	short day	long day	short day
Red larvae				
Larvae in treatments	10	12	13	9
Adults emerging	0	0	0	0
Non-red larvae				
Larvae collected November 4				
Larvae in treatments	16	16	18	16
Adults emerging				
Photuris A	2	6	16	14
Photuris B + D	1	4	2	1
Photuris V	—	1	—	1
Total	4[b]	11	18	16
Days to adult emergence[a]	128.3 AB	142.6 A	121.8 AB	114.4 B
Larvae collected December 6				
Larvae in treatments	8	7	7	7
Adults emerging				
Photuris A	6	7	7	4
Photuris B + D	—	—	—	1
Photuris V	1	—	—	—
Total	7	7	7	6[b]
Days to adult emergence[a]	81.7 B	111.2 A	82.9 B	81.2 B

[a] Differences between means followed by the same letter are not statistically different (*t* test, $P = 0.05$).

[b] Includes unidentifiable specimens.

Photuris V fireflies were reared from larvae collected throughout the year but were reared most frequently from larvae collected in wet areas at sites "M", "G" and "N" (Table 2). Most of the larvae collected on the roadside at Sites "G" and "N" produced *Photuris* V adults, whereas only a few of the larvae collected at Site "M" produced *Photuris* V adults.

EFFECT OF COLD TREATMENTS AND LIGHT CYCLES ON PUPATION: Of the 93 non-red larvae maintained in the photoperiod experiment 76 adults emerged (Table 3). The two light-dark cycles had no apparent effect on larvae reared at room temperature but adult emergence was significantly retarded for larvae in group 2 exposed to cold treatment and short-day photoperiod when returned to room temperature. Apparently the 2 factors acting together can delay pupation. Cold treatments also seemed to have a detrimental effect on the survival of these larvae.

None of the red larvae maintained in the photoperiod experiment pupated although they were reared well into the summer, long after the field populations

had emerged (Table 3). Of all the red larvae maintained during these studies only 2 pupated and produced adults (*P. congener*). Both of these fireflies emerged in March although one was collected in October and the other was collected in February.

McLean et al. (1972) reported that in Maryland they were able to induce larvae of *P. versicolor* and *P. lucicrescens* to pupate by exposing the larvae to 6–8 weeks of cold treatment or by exposing them to a 16:8 h light-dark cycle. K. Smalley (pers. comm.) was able to induce *Photuris divisa* (closely related to *P. congener*) to pupate using a 16:8 h light-dark cycle. She was unable to induce larvae of *P. missouriensis* McDermott to pupate even when exposed to various cold and light treatments. The factors controlling pupation in the red *Photuris* larvae remain a mystery. It seems unlikely that they would require a longer cold treatment since the field populations in Florida are not exposed to very severe winters.

Most of the larvae field collected between January and September pupated and adults emerged within 25–70 days. However, larvae collected in Oct., Nov., and Dec. pupated and produced adults after longer intervals of 60–140 days. The natural cool temperatures and short-day photoperiods in the fall had apparently induced fall-collected larvae to delay pupation. Pupation by larvae of *Pyractomena lucifera* (Melsh.) collected in the fall was also delayed when they were reared in short-day photoperiods but not when reared under long-day photoperiods (unpubl. data). McLean et al. (1972) found that emergence of adults from larvae collected in northeastern United States was delayed by cold treatments but the larvae responded readily to photoperiod treatments.

SOIL EXCAVATIONS: *Photuris* larvae spend inactive periods in several types of earthen chambers or excavations. Several variations were observed in the construction of "igloo" chambers (described by Hess, 1920). Chambers in which larvae molted were shallow and had ceilings that were 1.5–3 mm thick (Fig. 1A, B). Cells in which larvae pupated were deep and had ceilings that were 10–15 mm thick (Fig. 1C–G). Larvae sometimes remained inactive for extended periods in shallow cells and then resumed digging to form a deep cell in which they pupated. Larvae of *Photuris* A and B + D formed igloos with a rounded dome not much wider than the pupal chamber (Fig. 1C, D). These igloos measured 10–19 mm across and were raised 2–6 mm above the surroundings. Larvae of *Photuris* V formed igloos that were externally wider than the pupal chamber and were often flattened on top (Fig. 1E, F). These igloos measured 14–22 mm across and were also raised 2–6 mm above the surroundings. Larvae of *Photuris* "W" formed small pupal igloos similar to Fig. 1C and D but the ceiling was only 3–5 mm thick. Red *Photuris* larvae built both shallow and deep igloos as already described (Fig. 1A–D) but one larva formed a pupal chamber by burrowing into the soil and plugging up the opening with a mass of sand, without forming a true igloo (Fig. 1G). Larvae sometimes emerged from thin-topped igloos to feed but not from thick-topped ones.

Photuris larvae also made other excavations in the soil. When non-red larvae were placed in dishes with sand and filter paper some squeezed and burrowed under the paper to form a small chamber in which they rested during the day (Fig. 1J). Other non-red larvae dug small wedge-shaped holes in which they remained during the day (Fig. 1I). Some red larvae dug extensive burrows in the sand (Fig. 1H).

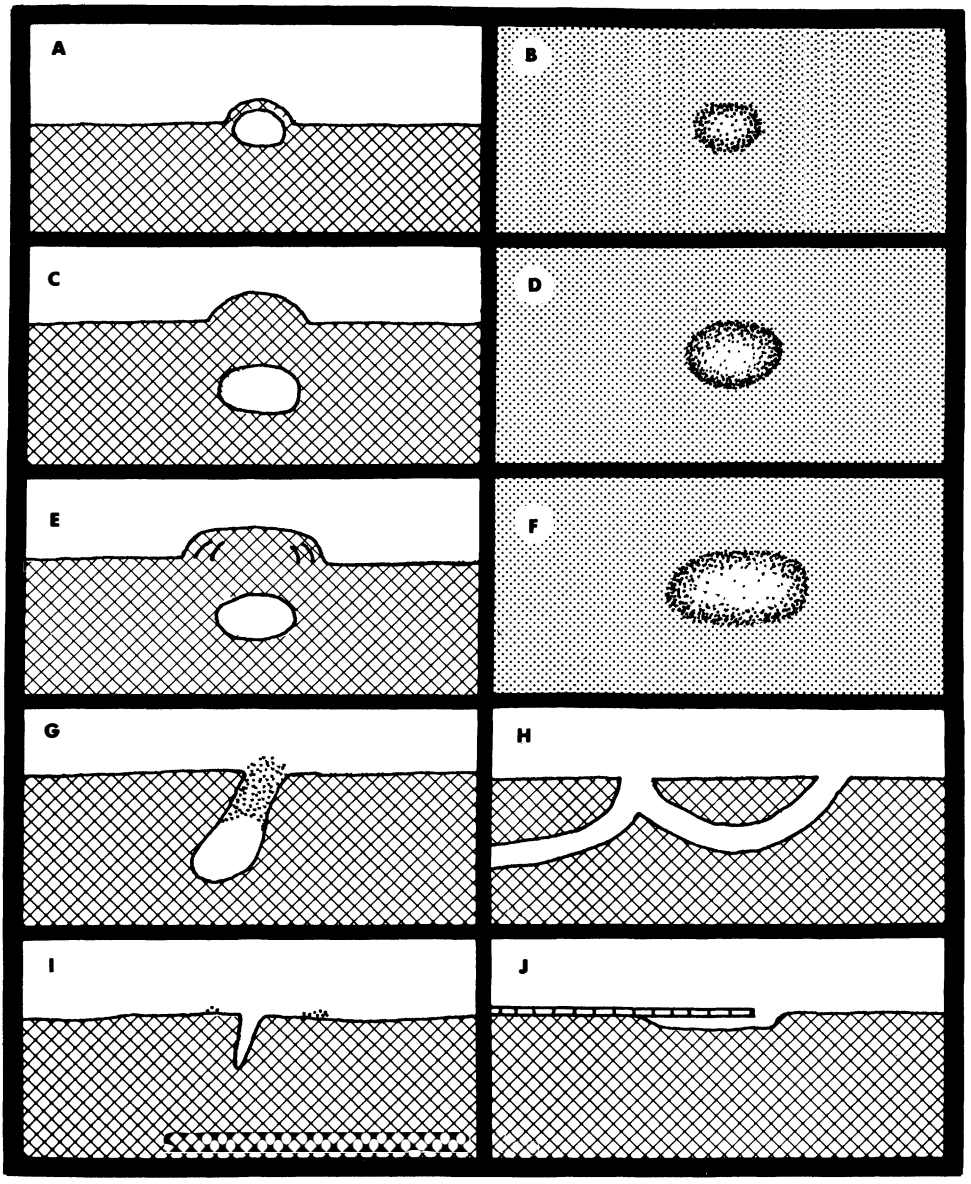

Fig. 1. Soil excavations by *Photuris* larvae: A and B, a molting chamber, cut away and surface views; C and D, a pupal chamber formed by a *Photuris* "A" larva, cut away and surface views; E and F, a pupal chamber formed by a *Photuris* "V" larva, cut away and surface views; G, a pupal cell formed by a red *Photuris* larva; H, burrows dug by a red *Photuris* larva; I, a wedge hole; and J, a burrow under paper.

Larvae took 1–3 days to build an igloo. When molting the larvae remained in the chamber for about 5 days before shedding the exuviae; the larvae emerged a day or so later. Initially larvae remained upright in their chambers. As long as they were in the upright position they would close a chamber if it was opened or they would build a new igloo if the old one was destroyed. Three to five days

before pupation the larvae turned over on their backs and remained in this position through the pupal period of 7 or 8 days. *Photuris* pupae were milky white and glowed brightly when disturbed. After the adult eclosed it remained in the earthen chamber 2–4 days. During this period the adult light organs gradually became functional and larval light organs gradually stopped functioning. Both light organs were functional simultaneously for a day or two.

LIFE CYCLE: The life cycle of *Photuris* larvae in the field is puzzling. Lloyd (1969) reports that he and D. Minnick obtained adult *Photuris* V in September from eggs laid in April. This suggests that if larvae develop continuously there could be 2 generations each year as observed in *Pyractomena lucifera* (unpubl. data). However, in the field the *Photuris* larvae can be found only in certain restricted seasons. At Site "N" (roadside) where *Photuris* V larvae seemed to predominate, larvae were observed only in August and September and again in January and February. They could not be found at other times of the year even when conditions were ideal. Similar seasonal occurrence was observed at other sites. The red larvae are observed August through November and were not observed at other times. If the larvae are active only these few months each year (and I do not imply that they are) it could take several years to complete development.

FEEDING BEHAVIOR: Information on the natural food of *Photuris* larvae is rather limited. Williams (1917) found 3 *Photuris* larvae feeding on a limp earthworm (which they had apparently killed). Hess (1920) found *Photuris* larvae feeding on snails on 2 occasions. McLean et al. (1972) reported they had "almost never seen them (*Photuris* larvae) feeding in the field." The list of items that *Photuris* larvae will eat in captivity is much longer (Williams, 1917; Hess, 1920; McDermott, 1958; Keiper and Solomon, 1972; McLean et al., 1972). They will kill and eat snails, slugs, earthworms, potato-beetle larvae, cutworm larvae and young squash-bug nymphs. They will also eat non-living food items such as cut-up insects, *Tubifex* worms, raw or cooked beef, pork or chicken liver, creamed cheese, boiled egg yolk, grapes, some vegetables and gelatin. I fed *Photuris* larvae various cut-up insects, cut-up earthworms and chicken liver.

I accumulated 21 food records for *Photuris* larvae in the field, 17 for red larvae and 4 for non-red larvae. These records can be summarized as follows: of the 17 records for red larvae, 5 were snails and slugs, 11 were insects of various kinds and 1 was a berry; of the 4 records for non-red larvae, 1 was an earthworm and 3 were berries. The snails were determined to be *Zonitoides arboreus* (Say) (Gastropoda: Zonitidae) and the slug was *Philomycus carolinianus* (Bosc) (Gastropoda: Philomycidae). The larvae fed on elderberries (*Sambucus* sp.) and wild grapes (*Vitis* sp.) that had fallen to the ground. Of the insects recorded as prey items 4 caterpillars of *Datana integerrima* (Grote and Robinson) (Notodontidae), 1 *Platycotis vittata* (F) (Homoptera: Membracidae) and 1 adult of *Oncideres cingulata* (Say) (Coleoptera: Cerambycidae) were discolored from decay indicating that the larvae were probably scavenging. However, *Photuris* larvae were also found attacking live insects on 5 other occasions: 3 larvae of *Plecia* sp. (Diptera: Bibionidae), a mycetophilid larva and a 4-cm caterpillar (Noctuidae: Herminiinae). The earthworm (Oligochaeta) was also a fresh kill.

Photuris larvae apparently prey on a variety of small soft-bodied organisms. However, they are also scavengers, feeding on a variety of non-living food items,

particularly dead insects and ripe berries. Most of my prey records involved red *Photuris* larvae and most of their prey items were insects. Non-red larvae were collected much more frequently than red larvae but were not observed feeding as often nor were they found feeding on insects.

Photuris larvae appeared to be very sensitive to the odor of injured caterpillars and other food items. In the laboratory, larvae were frequently observed walking directly to food items placed in their containers. When an uninjured caterpillar was placed with a group of larvae they paid little attention to it until it was injured by one of the larvae or with forceps. Then many larvae converged on the caterpillar and joined in the feast. In the field when injured caterpillars were placed near active *Photuris* larvae the larvae were usually attracted (4 of 6 times) and 2 larvae whose presence was previously unknown were also attracted. When a group of 10 freeze-killed and 10 injured (with a forceps) caterpillars were placed at random in the leaf litter in a red larvae habitat, 2 *Photuris* larvae were attracted to the wounded caterpillars, and none were attracted to the freeze-killed ones.

After a *Photuris* larva captured a prey item it continued chewing (and feeding?) for several minutes. When the prey was subdued, the larva released it and crawled for several minutes in the vicinity, then returned to the prey and dragged it to a location which it had just visited and continued feeding (5 observations). One *Photuris* larva was observed to lose its prey to an ant when the prey was left unguarded.

IDENTIFICATION OF LARVAE: If *Photuris* larvae could be determined to species without rearing them to the adult stage it would be much easier to study the field ecology and behavior of the different species. During these studies I was able to separate red from non-red larvae. The red larvae appeared to be larvae of *Photuris congener.* The dorsal pigmentation of the red larvae was reddish-brown or rufous with some black pigmentation. The non-red larvae produced all the other *Photuris* species. The dorsal pigmentation of these larvae was usually black with some gray or tan areas. The larvae collected in rotten logs producing *Photuris* W adults had large unpigmented areas on their tergites. These larvae could be separated from the other non-red larvae both by pigmentation pattern and site of collection. The remainder of the non-red larvae could not be separated reliably. It was noted that most of the largest and most robust larvae produced *Photuris* V and many of the larvae that had almost completely black tergites and dark sternites produced *Photuris* B + D but observations on these forms were too limited to be conclusive.

Since larvae of some species seem to predominate at certain collection sites and at certain seasons it would probably be useful to study larvae at different locations and seasons for comparative purposes until the morphological characteristics are better understood. It will probably require rearing larvae from adults of known identity to find morphological characters that could be used to identify larvae of additional *Photuris* species.

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